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VASCULAR ANATOMY OF ORCHID FLOWERS

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THAT the structural complexities of a flower can be made clear by a study of floral anatomy in relation to its vascularization is becoming a prevalent thought. While such a study is being concentrated on the members of several other natural orders, orchids, characterized by their "over-specialized" floral organization, still remain to be attacked from this angle.

Robert Brown (1831) was the first to elucidate the nature of the orchid flower. He compared it with the structural and other morphological features of the flowers of certain allied monocotyledonous families and interpreted the labellum as a compound structure made up of the lateral stamens of the outer whorl and the median petal. Darwin, after studying the course of vascular traces in a considerable number of orchid flowers belonging to different tribes, incorporated the results in his monograph, "The Various Contrivances by which Orchids are Fertilised by Insects" (ed. 1899). In general, he confirmed Brown's observations, particularly with regard to the compound nature of the gynostemium and labellum.

Subsequent to this publication, very little has been

published on the vascular anatomy of orchid flowers. Even this meagre information is confined to the study of only teratological material. The present study is an attempt to understand the structural complexities of normal orchid flowers.

Material and Methods

Vascular anatomy of the flowers of the following genera have been studied; the number of species investigated in this study is indicated by a digit in parenthesis after each genus:

	Diandrae	
Cypripedilinae		<i>Paphiopedilum</i> (2) <i>Cypripedium</i> (1)
	Monandrae	
Ophrydinae	Habenaria §	<i>Platanthera</i> (1) <i>Euhabenaria</i> (6) <i>Peristylus</i> (2) <i>Satyrium</i> (1)
Neottiinae		<i>Vanilla</i> (1) <i>Zeuxine</i> (1)
Coelogyninae		<i>Coelogyne</i> (2) <i>Pholidota</i> (1)
Liparidinae		<i>Oberonia</i> (2)
Phajinae		<i>Spathoglottis</i> (1)
Cyrtopodiinae		<i>Geodorum</i> (1) <i>Eulophia</i> (2)
Dendrobiinae		<i>Dendrobium</i> (3) <i>Eria</i> (1)
Bolbophyllinae		<i>Bulbophyllum</i> (1)
Cymbidiinae		<i>Cymbidium</i> (1)
Sarcanthinae		<i>Diploctrum</i> (2) <i>Luisia</i> (1) <i>Saccolabium</i> (3) <i>Vanda</i> (1) <i>Aerides</i> (2) <i>Rhynchostylis</i> (1)

Material was fixed in formalin-acetic-alcohol, and serial microtome sections of the entire flower buds were prepared following the customary methods. Basic fuchsin or crystal violet, with a counter stain of light green, was employed for staining the vasculature and ground tissue respectively. This combination gave satisfactory contrast.

In addition to sectioning, entire flower buds of some species were cleared first in chloral hydrate and subsequently in lactic acid. This method was especially suitable for small flowers (like *Oberonia*, *Diplocentrum*, etc.) and those with delicate floral parts (like *Zeuxine*, *Habenaria*, etc.). But for larger flower buds (*Cymbidium*, *Eulophia*, *Dendrobium*, etc.), a certain amount of trimming of the perianth was essential.

After observing both serial sections and cleared material, wire-plasticine models were constructed, and the three dimensional drawings reproduced here have been sketched from such models. The *vascular diagrams* that accompany the text have been drawn as seen from above; however, the exact places of origin of certain traces have been slightly exaggerated and spread out in one plane in order to bring out the details.

Structure of the Flower

The orchid flower is bilaterally symmetrical. The ovary is inferior and bears at its upper extremity the other floral organs. There are two whorls in the perianth, each whorl consisting of three members. Often, all the members of the outer whorl are similar in appearance, though sometimes the median member (often designated as the "hood" or the "dorsal sepal") may be somewhat more conspicuous than the lateral members either in pattern or size. In the inner whorl of the perianth, the two lateral members are usually small and of the same shape as those of the outer perianth members, whereas the median

one is almost always very dissimilar both in size and shape, and is known as the "lip" or "labellum." Next are two whorls of stamens, which present definite variations of expression in the two great subdivisions of the family, *Diandrae* and *Monandrae*. In the former, the two lateral stamens belonging to the inner whorl are functional, and the median one of the outer whorl is represented by a conspicuous staminode, which assumes various shapes. No indications of other staminal members can be made out externally. In the *Monandrae*, on the contrary, the median stamen belonging to the outer whorl is the functional one and no indications of the other staminal members are to be seen externally. In both groups the next and innermost whorl consists of three stigmas; in the *Diandrae*, all three are usually functional, whereas, in the *Monandrae*, only the two lateral are functional, the median one being modified as the rostellum. Furthermore, it may be noted that the stamens and stigmas in the *Diandrae* are almost "free," whereas in the *Monandrae* they are united into a central pillar-like structure, which has come to be known by the names "column" or "gynostemium."

In the present text and the accompanying figures I am using the following terminology and symbols for the various parts of the orchid flower (reference to Fig. 1 may be made):

Outer whorl of perianth	Dorsal sepal	DS
	Lateral sepals	LS
Inner whorl of perianth	Median petal (labellum)	MP
	Lateral petals	LP
Outer whorl of stamens	Median stamen	A1
	Lateral stamens	A2 and A3
Inner whorl of stamens	Lateral stamens	a1 and a2
	Median stamen	a3
Whorl of stigmas	Median stigma	G1
	Lateral stigmas	G2 and G3

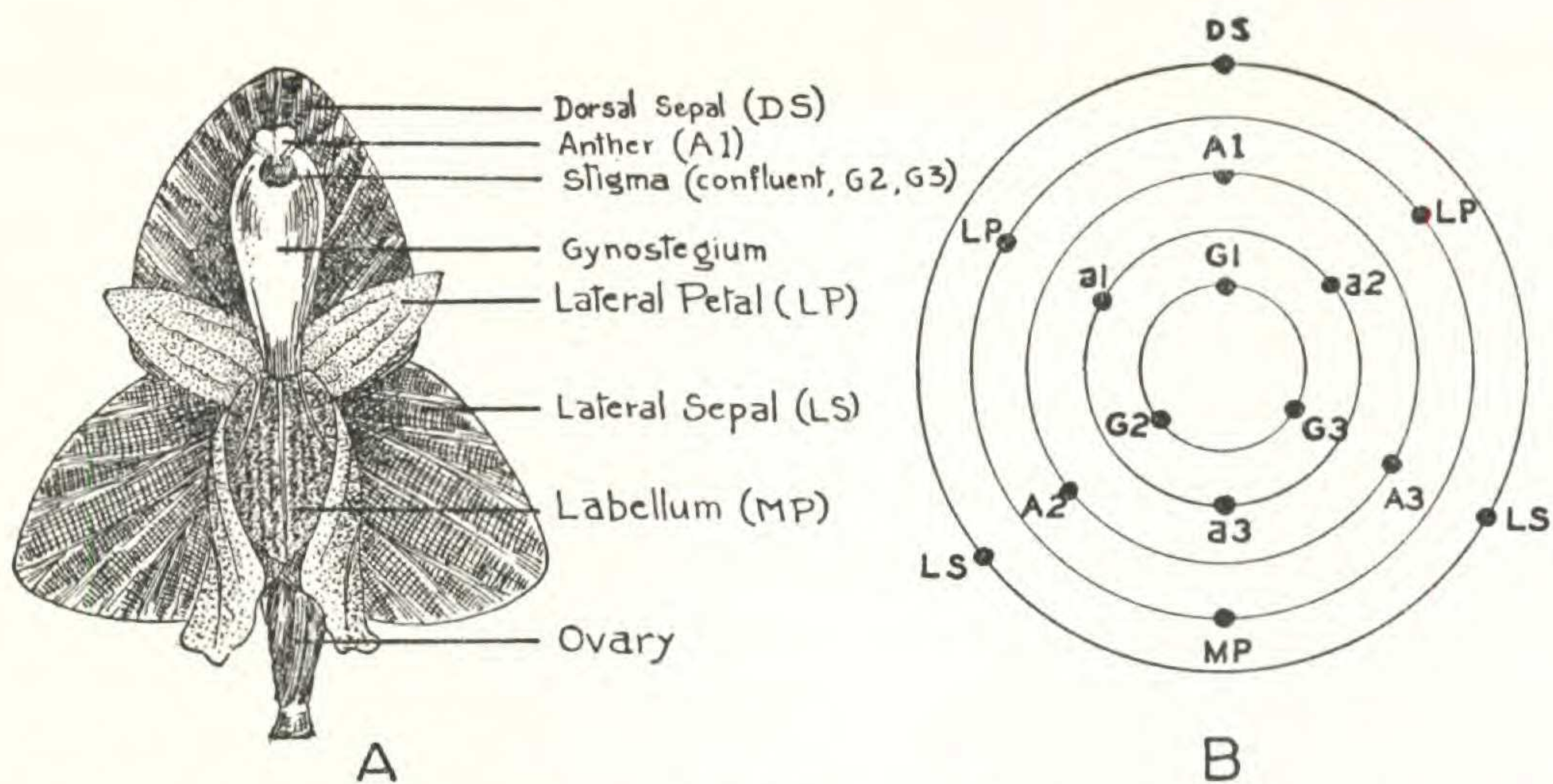


Fig. 1. A. A monandrous orchid flower showing its various parts.
 B. Ground plan of the various vascular traces of a generalized orchid flower to indicate the symbols used in the text.

The orchid ovary, as will be seen presently, is traversed by six main vascular traces,* each lying under a perianth member; I am applying to these traces the abbreviations corresponding to the perianth members.

Main Vascular Traces of the Ovary

In the inflorescence axis of the orchids the vascular bundles are arranged in the same scattered pattern as in the vegetative axis of monocotyledons. The number of bundles that enter the floral axis and their method of breaking up into the six main traces of the ovary vary considerably in different genera. In *Paphiopedilum* and *Cypripedium* of the Diandrae (Fig. 2 A), six vascular bundles from the inflorescence axis deviate into the flower and constitute the corresponding main traces (DS, two LS, two LP and MP) of the ovary. The bract is supplied by a seventh independent bundle (Br) from the inflorescence axis.

* The term *trace* is used throughout this text to designate the vascular elements in the flower from the moment the vascular *bundles* of the inflorescence axis enter the ovary.

Among the monandrous orchids, usually three bundles from the inflorescence axis deviate into the floral axis and while doing so break up into the six main traces of the ovary. The exact method of their breaking up varies among the different genera. Further, the different levels at which they break up is also variable to some extent within the same species. In *Habenaria* (Fig. 2 B), two of the three bundles that deviate from the inflorescence

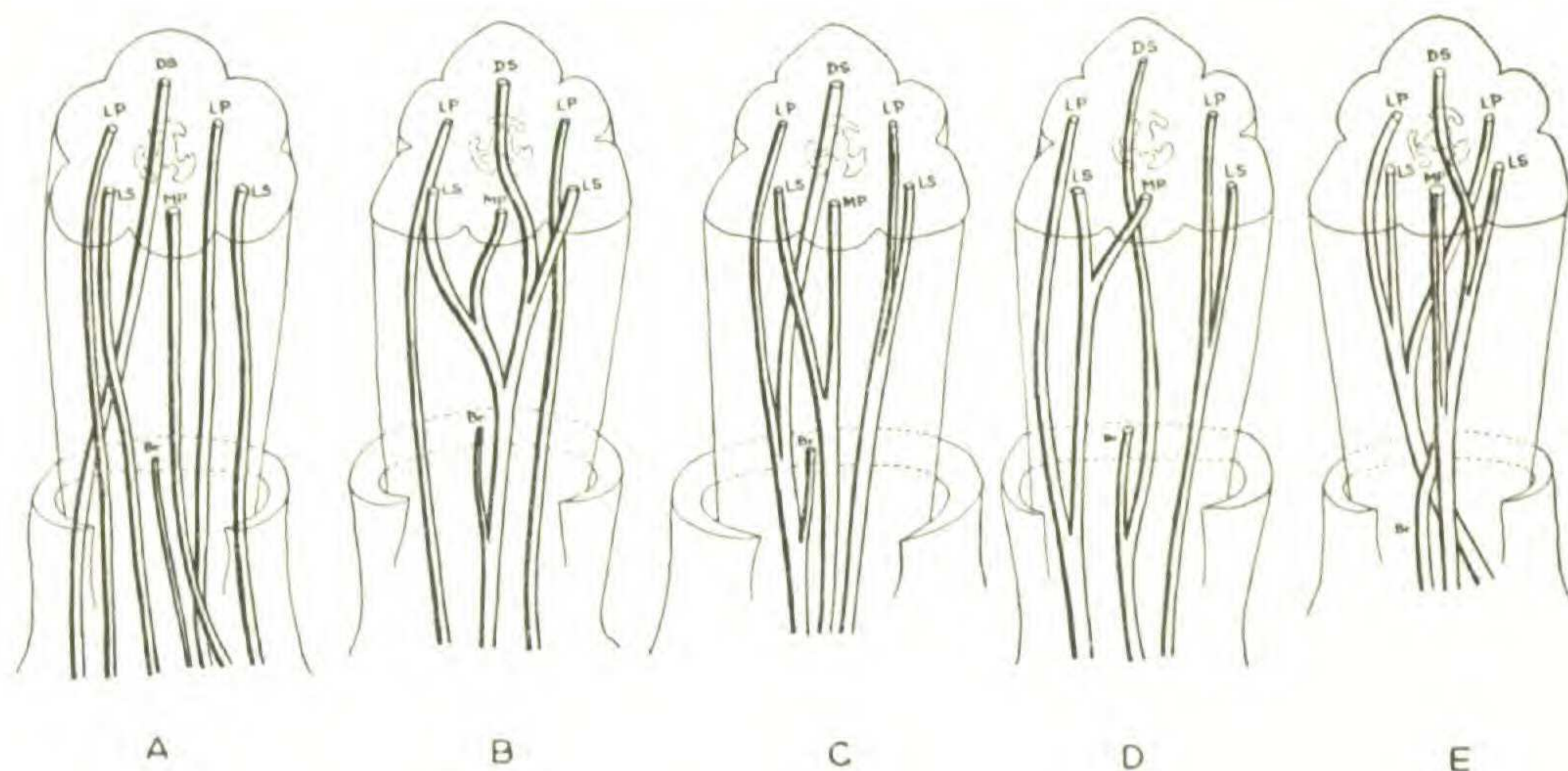


Fig. 2. A to E. Diagrams illustrating methods of the differentiation of the six main traces of the ovary from the vascular bundles of the inflorescence axis.

axis directly constitute those main traces of the ovary underlying the lateral petals (LP); the third bundle not only gives rise to the midrib trace of the bract (Br), but also, by further breaking up, constitutes the remaining four main traces of the ovary, underlying the dorsal sepal (DS), the two lateral sepals (LS) and the median petal (MP). In *Vanilla*, some species of *Dendrobium*, *Rhynchostylis* and a few others (Fig. 2 C), each of the three vascular bundles of the inflorescence axis that enters the flowers gives rise to two main traces of the ovary, the traces occupying positions under the adjacent perianth members (LP, DS; LP, LS; MP, LS); the median

trace of the bract (Br) is also given off by one of the three vascular bundles that deviates from the inflorescence axis. In *Bulbophyllum*, *Pholidota*, some other species of *Dendrobium* and a few others (Fig. 2 D), three vascular bundles from the inflorescence axis constitute the main traces of the ovary. One of the three breaks up into the median trace of the bract (Br) and the main trace of the ovary underlying the dorsal sepal (DS). The second, on bifurcation, forms the respective main traces underlying the lateral petal (LP) and lateral sepal (LS) of one side, whereas the third bundle gives rise to the remaining three main traces lying under the lateral petal (LP), the lateral sepal (LS) of the other side, and also to the median petal (MP). In *Cymbidium*, *Eulophia*, *Spathoglottis* and some members of the tribe Sarcanthinae (Fig. 2 E), though three vascular bundles from the inflorescence axis deviate into the floral axis, one of them constitutes only the midrib trace of the bract (Br). The second one gives rise to the main trace underlying the dorsal sepal (DS), one lateral sepal (LS) and median petal (MP). The third breaks up into the main traces underlying the lateral petals (LP) of both sides and the remaining lateral sepal. Thus in this instance only two bundles actually take part in the construction of the six main traces of the ovary.

The situation described above may be represented in the following tabular form (the vascular supply of the bract is omitted):

<i>Tribe or genera</i>	<i>Number of bundles deviating from the inflorescence axis into the floral axis</i>	<i>Method of further breaking up of the bundles of the inflorescence axis</i>
Cypripedilinae (Fig. 2 A)	6	No further differentiation; but directly constitute the six main traces of the ovary,—DS, LS, LS, LP, LP, MP.

Ophrydinae (Fig. 2 B)	3	1 (LP)+4 (DS, LS, MP, LS)+1 (LP)
<i>Vanilla, Dendrobium,</i> <i>Rhynchosyilis, Aerides, etc.</i> (Fig. 2 C)	3	2 (LP, DS)+2 (LP, LS) +2 (MP, LS)
<i>Oberonia, Bulbophyllum,</i> <i>Coelogyne, Pholidota,</i> etc. (Fig. 2 D)	3	3 (LP, LS, MP)+1 (DS) +2 (LP, LS)
<i>Cymbidium, Eulophia,</i> <i>Spathoglottis, some</i> members of Sarcanthinae, etc. (Fig. 2 E)	2	3 (LP, LP, LS)+3 (MP, LS, DS)

From the preceding account it will be clear that, from the standpoint of the origin of traces, there is no basis for distinguishing the main traces that belong to the outer whorl from those that belong to the inner whorl of the perianth. Actually, the bundles of the inflorescence axis that enter the flower split up in a variety of methods and constitute the six main traces of the ovary. Neither does there seem to be anything in the position of the traces themselves to distinguish the two whorls, because in transverse sections the six main bundles are arranged more or less on one and the same circumference (Fig. 3 A). There is also no difference between the traces of the two whorls with respect to size or degree of expression. Even those main traces that adjoin the placentae (LP, Fig. 3 B), which in other groups usually show an exaggerated development either in size or proliferation, in this case look exactly similar to the traces lying on alternating radii (DS, Fig. 3 B).

In some orchids with large-sized labellum (like *Cymbidium, Eulophia, Spathoglottis, etc.*) the main trace underlying this modified petal (MP) shows a double nature (Fig. 2 E). It may be argued by some that this feature may be due to the size-relation of the organ which it is supplying. The weight of this argument becomes

invalidated when we consider the fact that the corresponding trace in orchids like *Cypripedium* and *Paphiopedilum*, which possess labella of much larger size and display than those of *Cymbidium* or *Eulophia*, is always single.

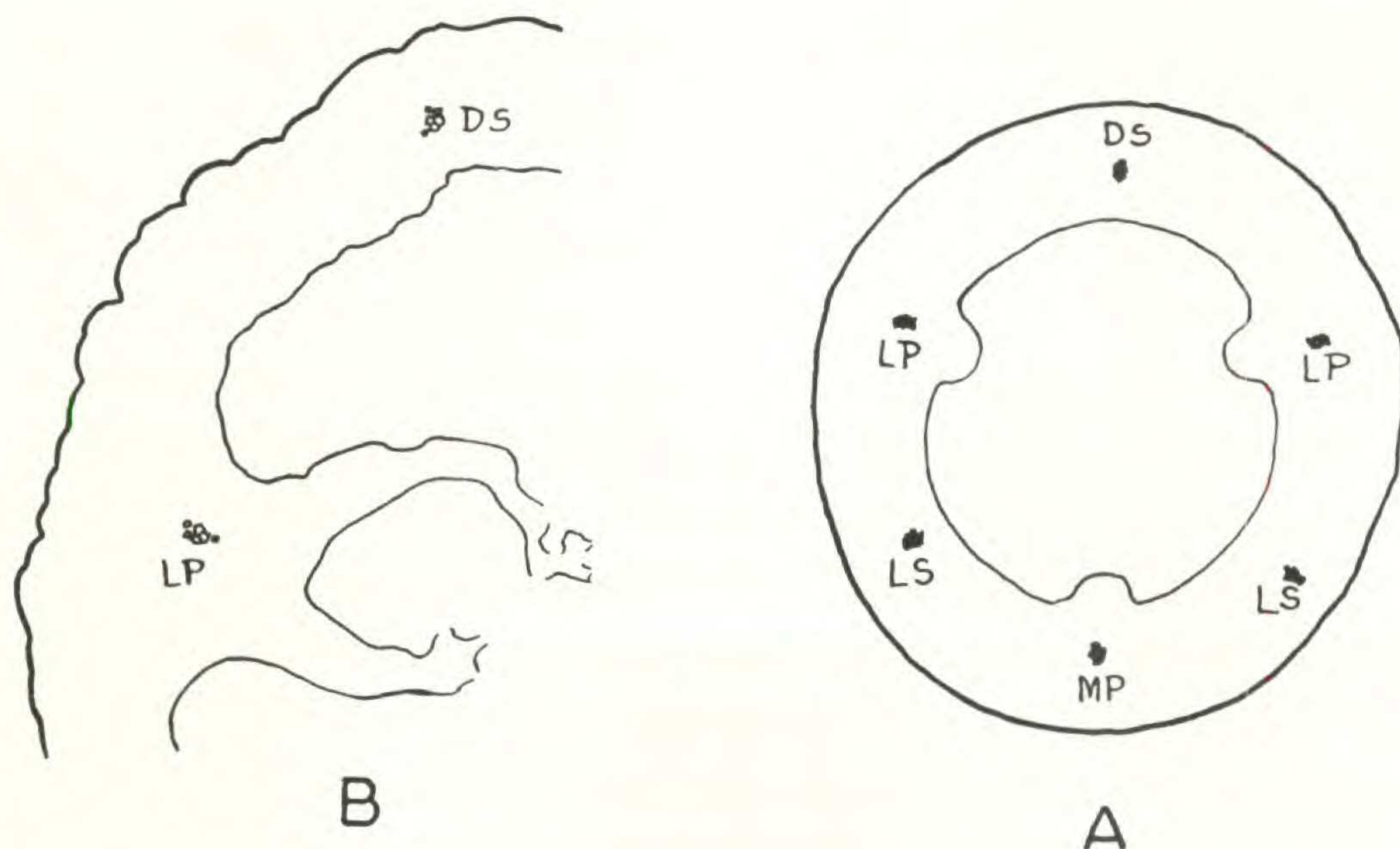


Fig. 3. A. Transverse section of an ovary showing the disposition of the six main vascular traces running in its wall. B. A portion of a transverse section of an ovary enlarged; traces DS and one of its adjacent LP are shown.

Another point which may be noted here is that the traces running along the placentae and underlying the inner whorl of perianth members do not show any signs of breaking up and supplying any part of the placentae. Hence the ovules are totally devoid of any kind of vascular supply.

Types of Vasculature in the Flower

The six main traces of the ovary begin to break up further into the various traces of the floral whorls and organs just below the level of insertion of the perianth. Though the general scheme of splitting is essentially the same in all the orchids investigated, three distinct types

may be recognized on the basis of the origin and nature of the vascular supply to the staminal and stigmatic whorls, rather than on the method of vascular supply to the perianth.

TYPE I. (Seen in the members of *Cypripedilinae*; Fig. 4 A, B and C). The traces to the median and lateral stigmas (G1, G2, G3) are the first to be separated. As can be expected, they arise from the main traces, DS and the two LS, underlying the median and lateral sepals respectively. At a slightly higher level, the same main traces trifurcate, to constitute the median and marginal traces of the respective perianth member. Further, the marginal traces of these sepal members supply the marginal traces to the petals also (Fig. 4 A). The main trace, DS, gives rise to another small trace (A1) at a slightly higher level; this trace runs vertically into the staminode.

The main traces occupying positions under the lateral perianth lobes of the inner whorl, after giving out the traces to the functional stamens (a1 and a2), merely pass into the respective petal as its median trace. The marginal traces of these, as has been stated, are derived from branches of marginal traces of the sepal members. The main trace, MP, does not split up but continues into the labellum as its median trace.

The following points may be especially noted in this connection:

1. Masters (1887) observed in some species of *Cypripedium* that the trace underlying the labellum also trifurcated to form the median and marginal traces of that petal. However, the flowers here examined do not show this feature. The marginals of the labellum are always given out by the marginal veins from its adjacent sepal members.

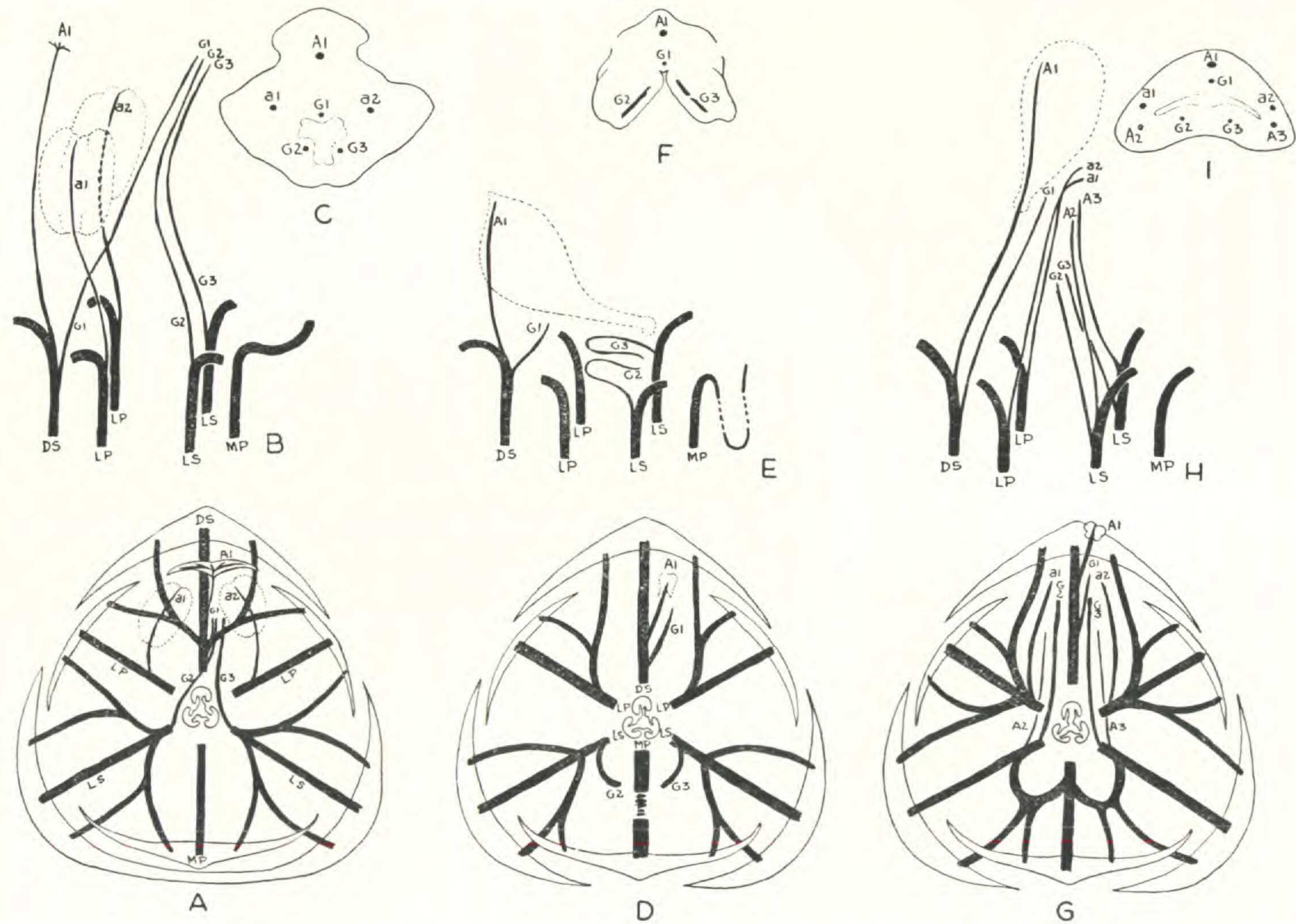


Fig. 4. A, B and C. *Paphiopedilum*. D, E and F. *Habenaria*. G, H and I. A monandrous orchid. A, D and G are vascular diagrams; B, E and H are drawings from wire-plasticine models; C, F and I are transverse sections at the region homologous with the gynostemium.

2. The vascular traces supplying the staminode, functional stamens and stigmas, all run only for a very short distance in a common tissue; hence a definite structure like the gynostemium is almost absent or highly reduced in these plants. However reduced this structure may be, the following six vascular traces may always be recognized in a transverse section (Fig. 2 C):

- a. A 1 occupying a dorsal median position,
- b. a 1 and a 2 occupying a lateral position, and
- c. G 1, G 2 and G 3, all three together occupying a place just below A 1.

3. Link (1849) thought that the fertile lateral anthers of *Cypripedilinae* originated by the division of the median stamen, the staminode being looked upon as an enormously developed connective. Masters' observations on teratological material have already cast a doubt on the tenability of this view. The present studies also suggest that Link's interpretation is erroneous.

TYPE II. (Seen in the members of *Ophrydinae*; Fig. 4, D, E and F). The main trace, DS, gives rise to the traces that supply the median stigma (G 1), the median stamen, A 1, and the median trace of the corresponding sepal. The marginal traces for this sepal are supplied by the main traces underlying the lateral petals (LP). The main trace (MP) does not give rise to any other trace excepting the median one of the labellum and its spur, which is merely a downward pouch-like extension of the labellum; the marginal traces are supplied by those of the adjacent perianth lobes of the outer whorl (LS). The main traces underlying the lateral sepals, in addition to forming the median and marginal traces of these lobes, give rise to the traces, G 2 and G 3, which supply the lateral stigmas.

It may also be noted that the marginal traces of the

lateral petals are altogether absent in *Habenaria* § *Platanthera*; the marginal traces towards the dorsal sepal alone are present in *Habenaria* § *Peristylus*; and in some species of *Euhabenaria*, their presence is occasional and often they are very poorly developed.

A transverse section passing through the gynostemium at the level of the stigmas (Fig. 4 F) shows the following four vascular traces:

- a. A 1, representing the supply to the functional stamen (median) of the outer whorl, and
- b. G 1, G 2 and G 3, supplying the median and lateral stigmas respectively.

Generally the members of Ophrydinae possess a spur. Morphologically this structure is nothing but a downward outgrowth of the labellum in the form of a long tube or sac. *Satyrium nepalense* has a double spur; it is also dorsal in relation to the inflorescence and flower, as there is no resupination. Where the spur is single, the median trace of the labellum runs throughout its entire length and finally continues upwards into the labellum (Fig. 5 A). The marginal traces of the labellum (that are derived from the adjacent sepal traces), however, do not enter the spur but curve up into the expanded portion of the labellum (Fig. 5 A). On the other hand, where the spur is double, the median trace of the labellum does not enter the spur but runs straight into the median petal as its median trace; the marginal traces (that are given off by the adjacent sepal traces) run throughout the length of the spur on that side and then continue into the median petal as its marginal traces (Fig. 5 B).

TYPE III. (Seen in the majority of monandrous orchids. Fig. 4 G, H and I). The first traces to be separated off at the level of insertion of the perianth are those to the three stigmas (G 1, G 2 and G 3), given off by the

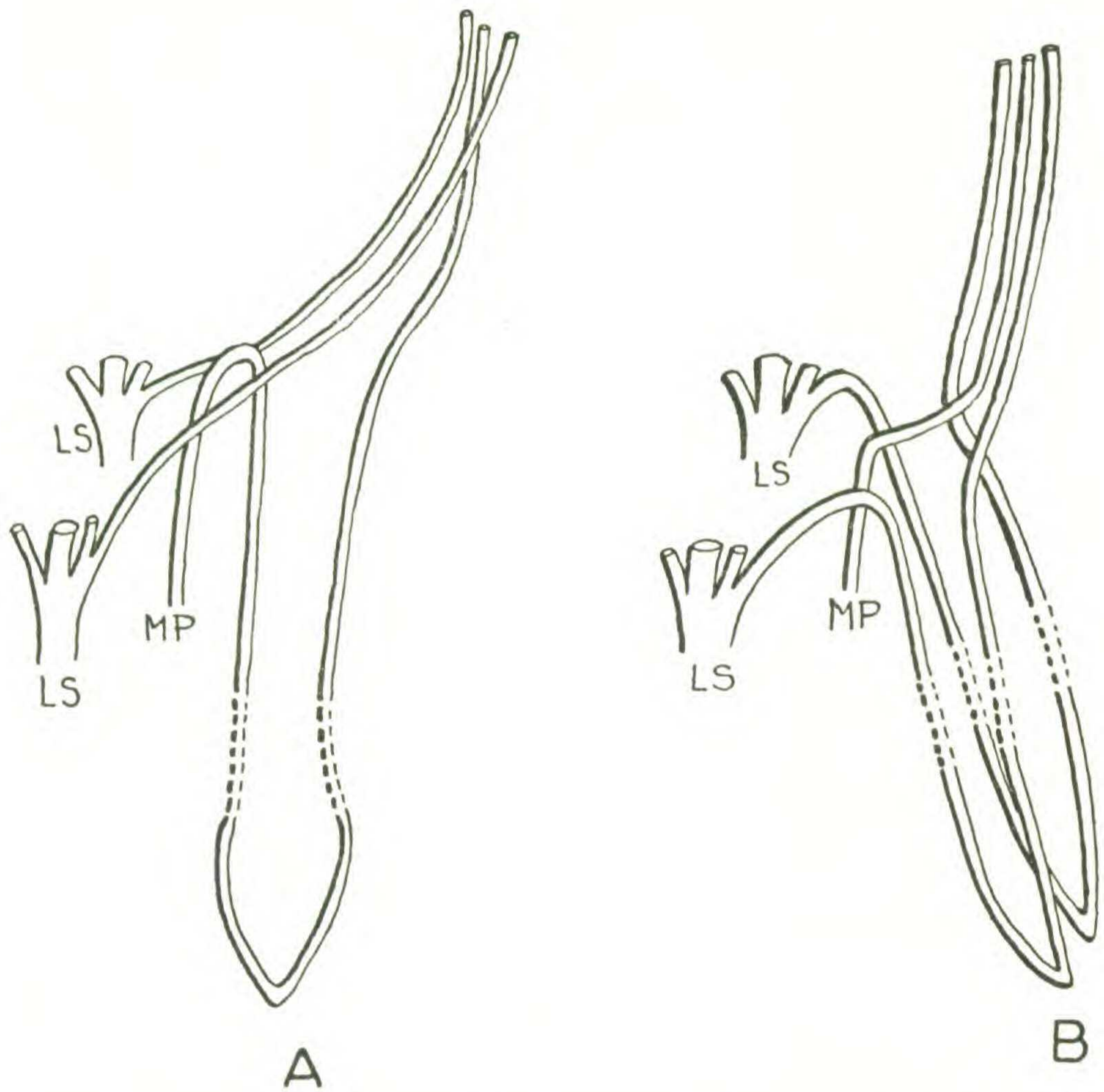


Fig. 5. Drawings from wire-plasticine models to illustrate the nature of the vascular supply to the labellum and spur.

A. When the spur is single; B. When the spur is double.

main traces underlying the sepals. Then, in some genera, each of the main traces underlying the lateral petals (LP) gives off a trace (a1 and a2) into the gynostemium, these representing the lateral stamens of the inner whorl. In some other genera, the main traces of the lateral sepals (LS) each give out a trace (A2 and A3) into the gynostemium; these represent the traces belonging to the lateral stamens of the outer whorl. The commoner condition is the presence of the traces representing the lateral stamens of the inner whorl. In some genera (*Dendrobium*,

Cymbidium, etc.), both sets of lateral stamens (A 2, A 3 and a1, a2) may be present. It must be stated here that the expression of the staminal traces is highly variable in different genera and is often associated with highly complicated types of adnation. (This phenomenon is treated in detail in a later part of this text under "Comparative Resumé of the Vascular Supply of the Stamens." See page 77). After supplying the vasculature to the stamens and stigmas, the residue of the main traces (excepting the one under the dorsal sepal) breaks up further to constitute the vascular traces of the perianth lobes. (Variations of the vasculature of the perianth members of this type are explained in a later part of this text under "Comparative Resumé of the Vascular Supply of the Perianth." See page 76).

The following points may be noted in connection with this type:

1. The gynostemium (Fig. 4 I) contains the following traces:

- a. A 1 supplying the median stamen of the outer whorl, which is the functional one,
- b. G 1, G 2 and G 3, reaching the rostellum and the confluent lateral functional stigmas, and
- c. either a 1 and a 2 representing the traces of the lateral stamens of the inner whorl, or A 2 and A 3 representing the lateral stamens of the outer whorl, or both.

2. The traces of the staminal and stigmatic whorls are all embedded in a well-developed pillar-like structure (a gynostemium).

Types I and II are consistent; no marked variations were seen. But Type III is subjected to a high degree of plasticity. This is closely associated with increasing cohesion, adnation and other phenomena which are described in the following paragraphs.

*Comparative Résumé of the Vascular Supply
of the Perianth*

In minute flowers like those of *Oberonia* and in the flowers of the semi-saprophyte, *Zeuxine*, the vasculature is very poorly developed. As a result, the system is not attended by any secondary modifications (Fig. 6, B). In flowers like those of *Vanilla*, *Coelogyne*, etc., the marginal traces of the adjacent perianth members lie close together (Fig. 6 C). In *Dendrobium*, *Bulbophyllum*,

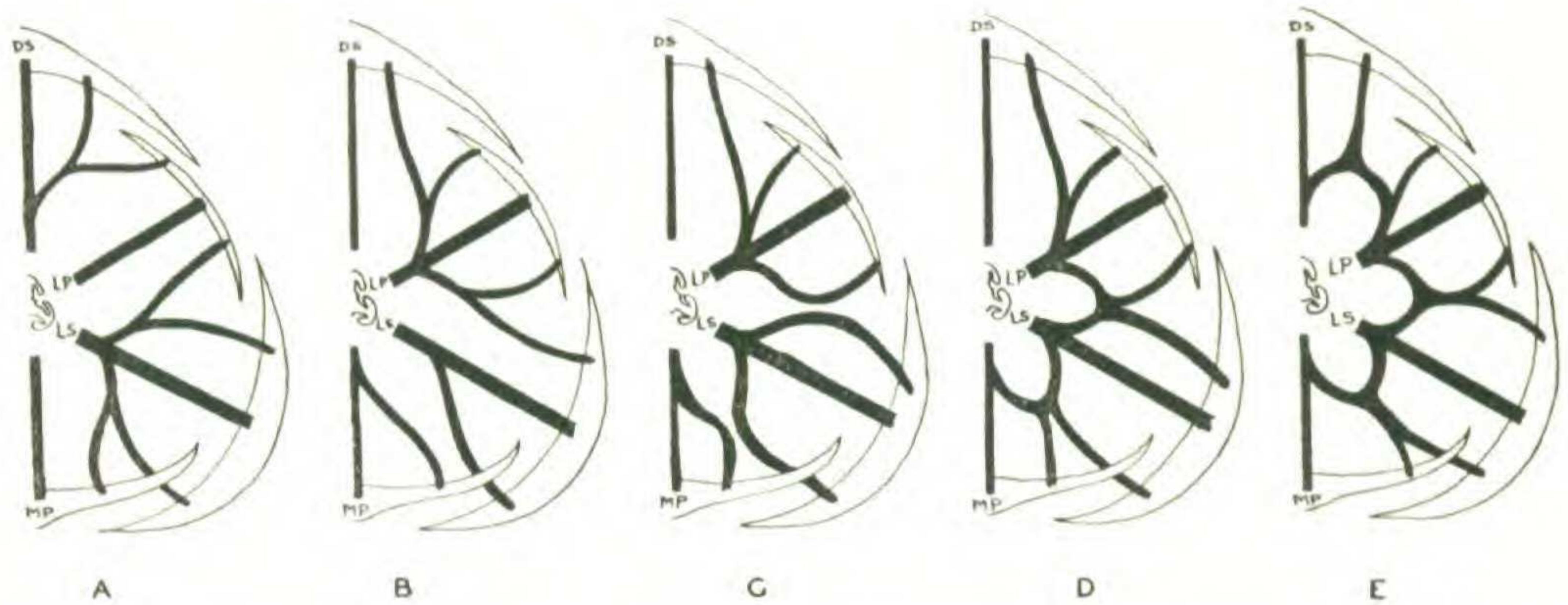


Fig. 6. A to E. Series of diagrams to illustrate the increasing complexity of the vascular supply of the perianth members. Only one-half of the flowers is shown; traces to the stamens and stigmas are not shown for the sake of avoiding confusion.

Pholidota, *Spathoglottis*, etc., the marginal traces fuse to form an "arch" and from this point again separate out (Fig. 6 D). In *Cymbidium* and many members of the tribe Sarcanthinae, the marginal traces after forming an "arch" proceed in a fused condition for a considerable distance and then separate (Fig. 6 E). Often some of the marginal traces even enter the respective perianth member in the fused condition (see the marginal trace of the dorsal sepal in Fig. 6 E).

It may also be noted that the main trace, DS, does not in general give rise to any of the marginal traces of the dorsal sepal. But when it does split up into the marginal traces, as in *Cymbidium* and some members of the Sar-

canthinae, it invariably anastomoses with those of the adjacent lateral petal.

Another feature to be noted is the origin of the marginal traces of the adjacent perianth lobes. Usually the marginal traces of the outer perianth members are derived from the traces underlying the perianth members of the inner whorl or *vice versa*.

Comparative Résumé of the Vascular Supply of the Stamens

A lack of proper understanding of the vasculature of the staminal whorls, in the past, seems to have been the cause of the confusion prevailing today with regard to the exact composition of the androecium of orchids. In this connection two points need clarification, — (A) the number of staminal traces that are given off and their identity, and (B) the method by which a simple origin becomes increasingly complicated through the intervention of adnation. It is difficult to separate the two aspects which are so closely associated in orchids; but for the sake of convenience of description, I propose to treat the two points under the headings (A) and (B), as mentioned above.

A. It has already been pointed out that in the Cypripedilinae the two lateral stamens of the inner whorl (a1 and a2) are functional and that the median stamen of the outer whorl (A1) is externally represented by a staminode, which also receives a vascular trace. Furthermore, it has also been mentioned that in the monandrous orchids it is the median stamen of the outer whorl (A1) that is functional and that quite often the lateral stamens of the inner whorl (a1 and a2) are represented only by vascular traces. The presence or absence of the traces cannot be made out by any external morphological distinctions.

It may be recalled that in some species the traces for the lateral stamens of the outer whorl (A2 and A3) may also be represented and that in many instances all of the four lateral stamens may be represented by their corresponding vascular traces in varying degrees of expression: that is, the traces themselves may be so rudimentary that they do not run even to the base of the gynostemium, or they run up only a short distance into the structure, or they may even reach the distal end of it. The degree of expression may affect one, two, three or all of the four lateral staminal traces. The latter condition may be frequently seen in *Zeuxine*, *Oberonia*, *Eria*, etc.

Clear-cut examples where either the lateral stamens of the inner whorl alone or only those of the outer whorl manifest themselves are seen in *Eulophia*. In *E. nuda* (Fig. 7 A and B) the main traces (LS) underlying the lateral perianth members of the outer whorl, after giving off the traces G2 and G3 to the respective stigmas, separate out correspondingly the traces A2 and A3. That

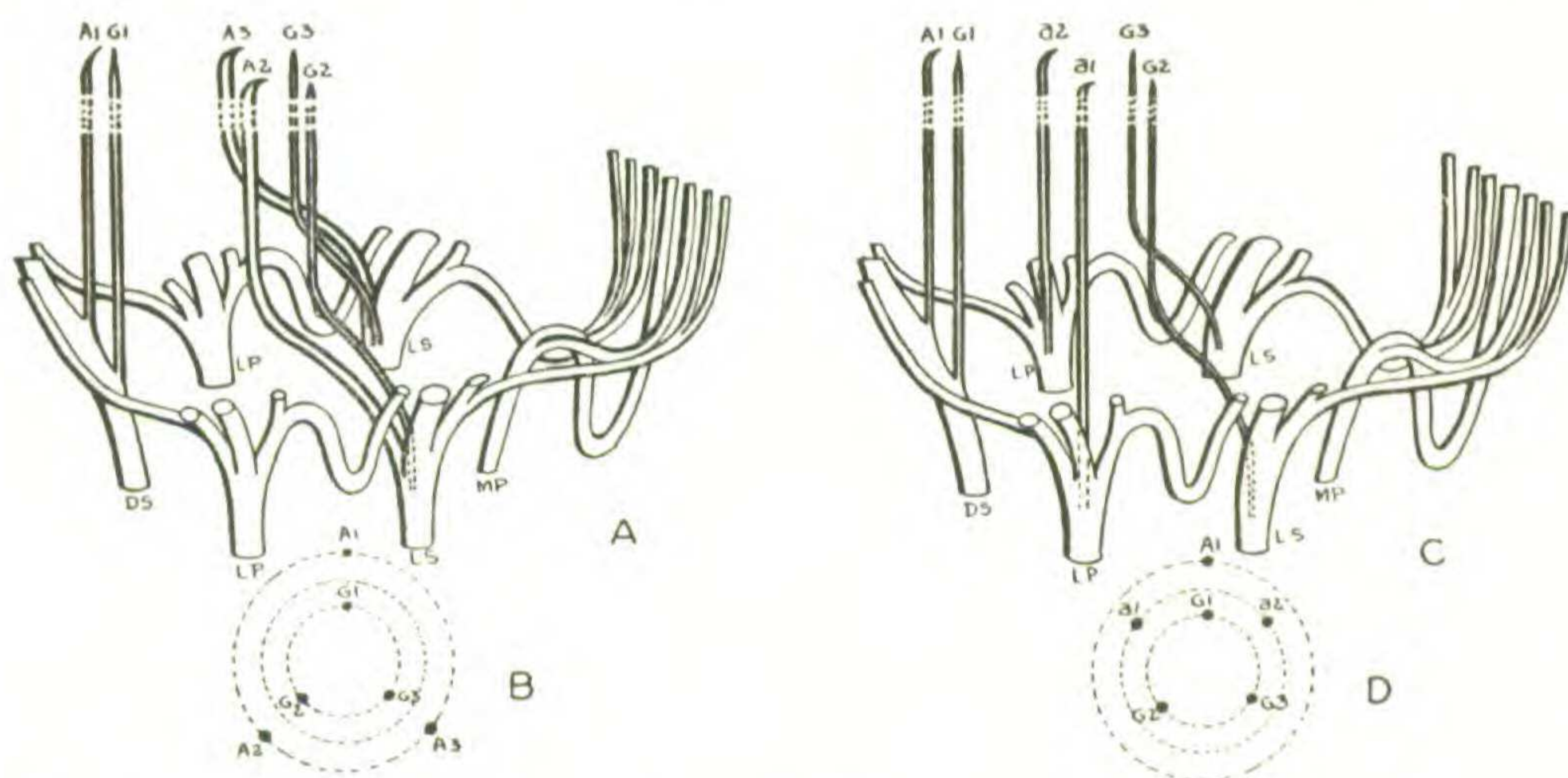


Fig. 7. Drawings of vascular skeletons made from wire-plasticine models illustrating the splitting up of the six main vascular traces of the ovary into the vascular supply of various whorls. A and B. *Eulophia nuda*; C and D. *Eulophia epidendreaea*. In B and D the staminal and stigmatic traces are shown as rearranged according to their status; vascular traces of the perianth members are omitted in these.

these traces represent only the lateral stamens of the outer whorl and that these cannot be considered to be otherwise is proved by the fact that they originate after the stigmatic traces have been separated off and before the trifurcation which results in the formation of the median and marginal traces of the respective perianth member. In *E. epidendreaea* (Fig. 7 C and D), the main traces, LP, underlying the lateral petals, before splitting up to form the supply to the corresponding perianth members, give out the traces a1 and a2 which obviously represent the traces for the lateral stamens of the inner whorl. That these traces cannot be interpreted otherwise is borne out by the point of their separation from the main trace, LP.

B. In other orchids, the degree of expression of the traces for the stamens of the two whorls is complicated by the associated phenomenon of adnation. The series of diagrammatic illustrations in Fig. 8 is intended to convey the increasing complexity in the origin of the staminal traces. In these figures the behavior of one pair of the main traces (LP and LS) underlying the lateral perianth members of one side of the flower is shown. A illustrates the simplest condition where there is no fusion; the staminal traces a2 (belonging to the inner whorl) and A3 (belonging to the outer whorl) are quite distinct both in origin and further course. In B, the two traces are still distinct; but their separation from the respective main traces is postponed until after the trifurcation of the main traces themselves; thus the position of the origin of the staminal traces is carried up to a higher level in relation to the floral axis. In C, the position of origin of the two staminal traces is carried up still higher; they originate at a point nearer to the anastomosing point of the marginal traces. Furthermore, the two staminal

traces come to lie closer soon after separation and seem to fuse with one another and then proceed upwards in the gynostemium. D illustrates the climax of this tendency. The origin itself of both the staminal members is carried higher to a point where the adjacent marginal traces fuse and thus their distinctness becomes totally obliterated. Further, the marginal traces of the respective perianth

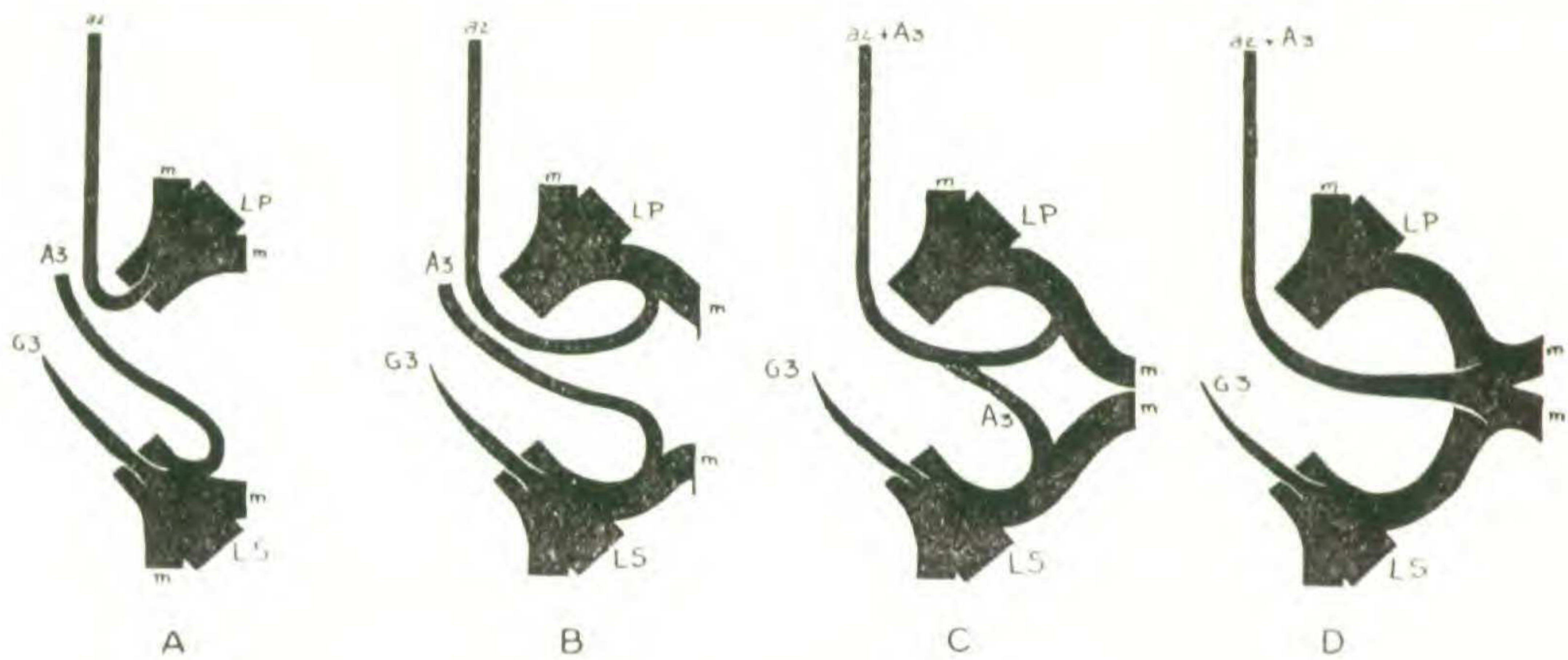


Fig. 8. A to D. Diagrams to illustrate the evolution of "compound" staminal traces, $a_2 + A_3$.

member are also separated from the same point. Thus the nature of the staminal trace in this instance becomes "compound" by the adnation of a lateral stamen of the inner whorl with that of a lateral stamen of the outer whorl, and as a consequence such traces have been here interpreted and represented as $a_1 + A_2$ or $a_2 + A_3$, as the case may be.

The degree of expression of adnation is often seen to vary in one and the same species. *Geodorum densiflorum* may be taken as a good example to exhibit this phenomenon; furthermore, this orchid also throws some light on the fundamental nature of the androecium of the family. Normally in this species, in addition to A_1 , the lateral stamens of the two whorls are also represented by "compound" traces, $a_1 + A_2$ and $a_2 + A_3$ (Fig. 9 A and B).

As has been stated more than once, the vascular pattern is not always strictly fixed, but is somewhat plastic in this species. In all of the three instances of deviations to be described below, the origin and nature of the trace A1 is very consistent, as in the other monandrous orchids. It is the nature of the other vascular traces of the staminal whorls that present interesting variations. In the first deviation (Fig. 9 C and D) the staminal vascular traces arise from the point of trifurcation of the main traces, LS. Thus the traces A2 and A3 complete the outer whorl of stamens. In the second deviation (Fig. 9 E and F), the main trace under one of the lateral sepals give rise to the trace A2 (representing a lateral stamen of the outer whorl), whereas on the opposite side the main trace lying under the lateral petal gives the trace a2 (representing a lateral stamen of the inner whorl). In the third deviation (Fig. 9 G and H, left), there arises a compound staminal trace, a1+A2, whereas on the opposite side the main trace under the lateral sepal gives rise to A3, representing a lateral stamen of the outer whorl). In addition to these two, the main trace, MP (lying under the labellum), also sends out a slender offshoot, a3, into the gynostemium; this trace is to be interpreted only as representing the median stamen of the inner whorl. Thus, these deviations, when taken together, reveal the presence of all of the six stamens belonging to the two whorls. This also makes it possible to visualize the fact that all of the six stamens were once functional in the ancestral orchid flower.

In passing, it may also be noted by a study of these illustrations (Fig. 9) that the plasticity of vasculature is not confined to the staminal whorls alone but is extended to the labellum also, whereby the latter is supplied by supernumerary marginal traces in certain instances.

Before proceeding to the general discussion, it is im-

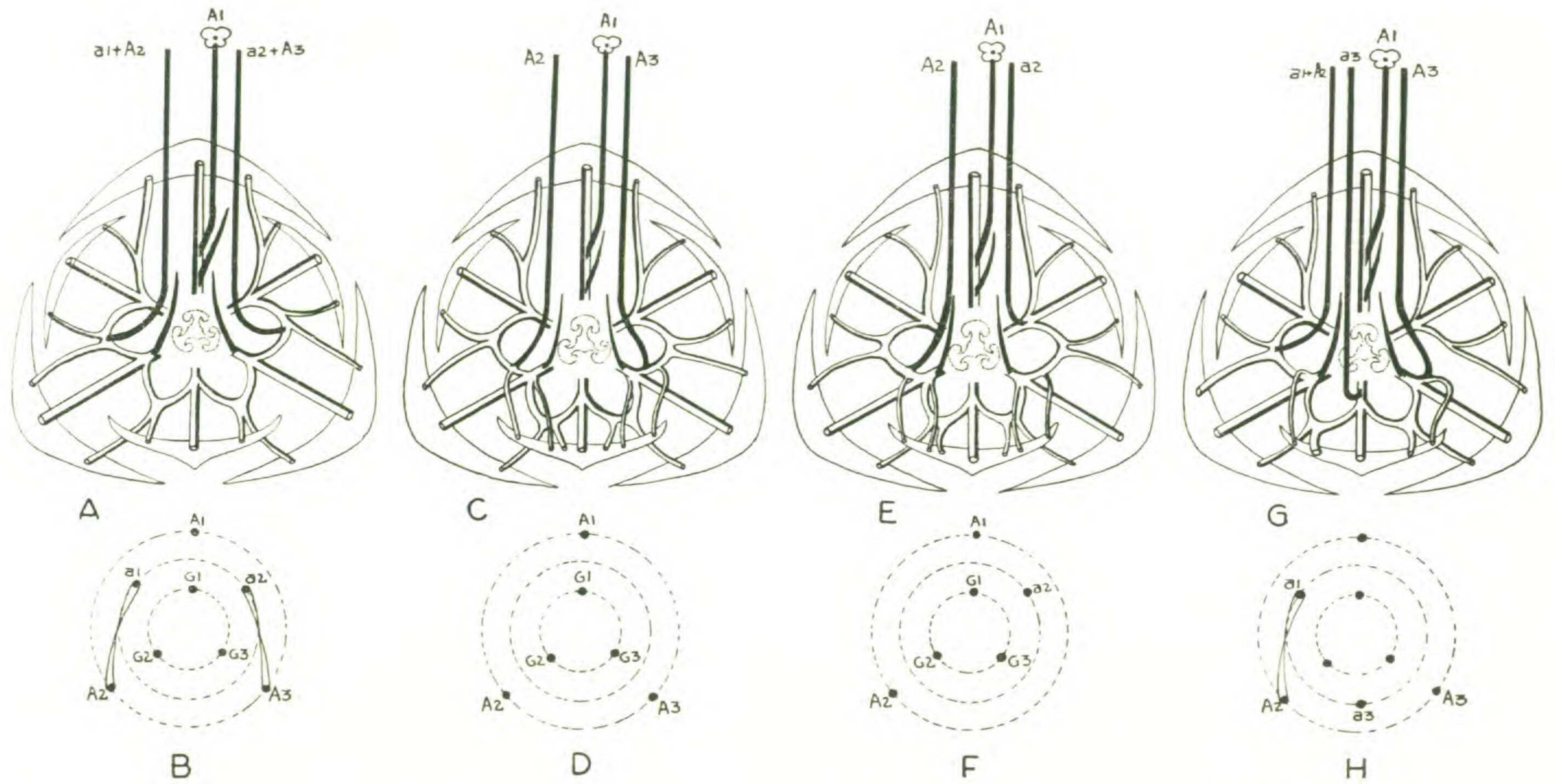


Fig. 9. A, C, E and G. Vascular diagrams of the normal and three deviation patterns respectively of *Geodorum densiflorum*. Traces belonging to the stamens and stigmas are shown in solid black. B, D, F and H. Staminal and stigmatic traces of A, C, E and G respectively, arranged according to their status.

portant to have an idea of the changes that are brought about in the vascular pattern of the flower during the development of the flower itself. This type of study was confined only to *Dendrobium* and *Cymbidium*, but I feel that the results obtained may in general be applicable to other orchids also. Here again, particular attention may be laid upon the development of "compound" staminal traces.

In the young condition (when the microsporangium is just differentiated) the marginal traces of the adjacent lateral petal and sepal show the following features (Fig. 10 A): The staminal traces a_1 , a_2 , A_2 and A_3 are all distinct from one another, although their place of origin is shifted higher up to the point of concrescence of the adjacent marginal traces; but actual concrescence is not yet affected. During subsequent development, concrescence and adnation proceed to such a degree that the distinct origin of the staminal traces becomes totally obliterated so that they are seen only as "compound"

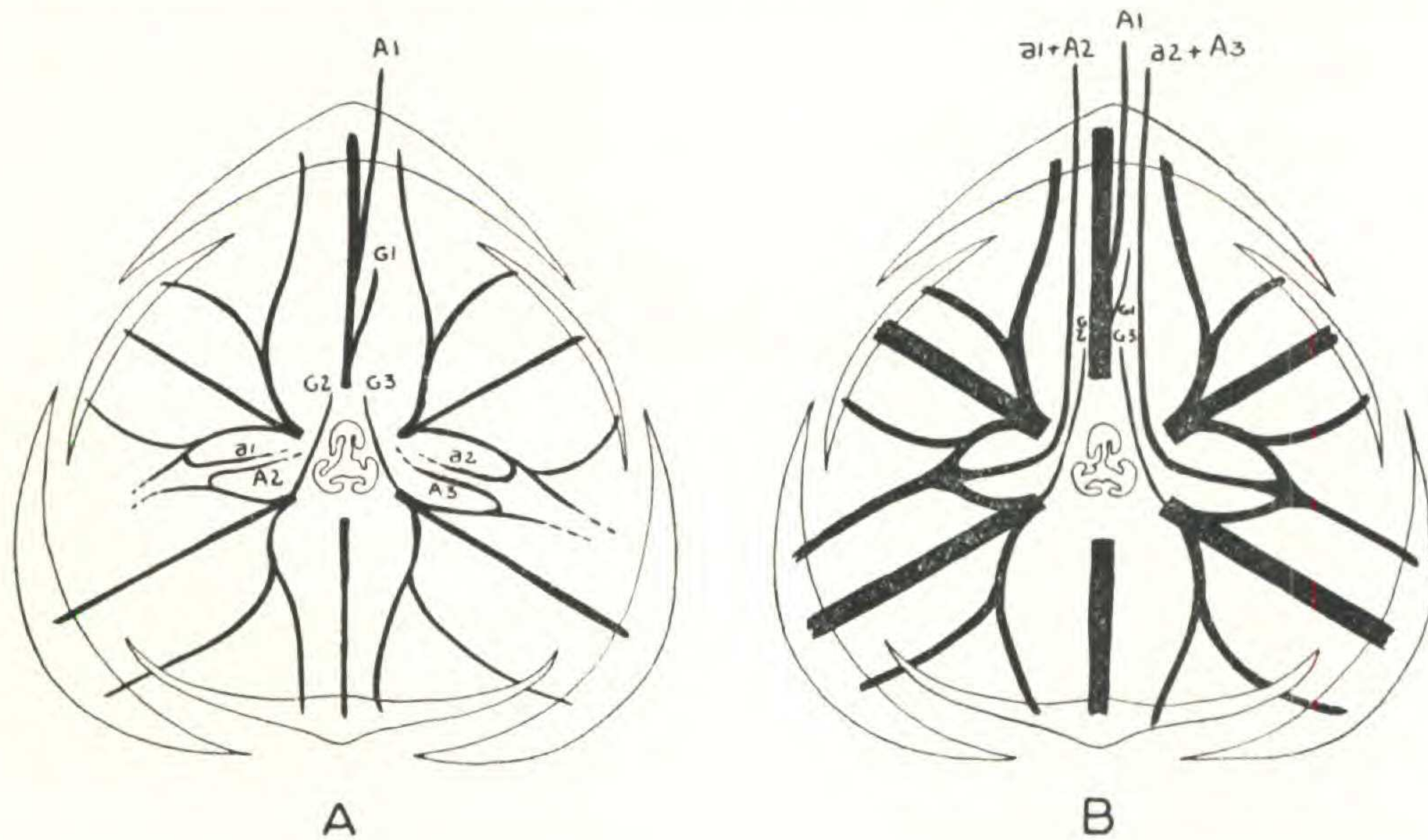


Fig. 10. Vascular diagrams of *Dendrobium* showing the juvenile condition in A and the adult condition in B.

traces (Fig. 10 B); thus the traces for adjacent lateral stamens of the one side are represented by the compound trace, $a1+A2$, and on the other side by the similar trace, $a2+A3$.

General Discussion

OVARY. In recent years the nature of superior and inferior ovaries has raised a good deal of controversy. The evidence at hand points out that the inferior ovary in at least the majority of instances is a product of adnation of floral whorls, though there seems to be some evidence as to its receptacular nature in a few genera or groups of plants. The orchid ovary, as has been said before, is traversed by six main vascular traces that run throughout the length of the ovary proper without any kind of splitting, and the further division begins only at about the insertion level of the perianth and other floral organs. This condition may be looked upon as a result of adnation in its extreme degree of expression. The irregularity seen in the method of origin of the six main traces of the ovary in different genera of orchids may also be correlated in some way with the high degree of adnation.

PERIANTH. The whorls of perianth members externally suggest considerable distinctness. In general, those of the outer whorl are uniform in appearance, whereas those of the inner whorl are variable. Particularly does the labellum (median petal) assume a series of varied patterns in size, shape and color. Whatever may be the outward manifestation, internally each of them (sepals as well as petals) receives a median and two marginal traces. Quite often the marginal traces of one whorl of the perianth members are derived from the traces belonging to the perianth members of the other whorl. Anatomically, all of the perianth members are thus of the

same category. The 3-trace supply is more a characteristic feature of sepals than of stamens. From these considerations, the perianth of orchids seems to be more sepaline in character.

Ontogeny of the flower, in some cases, has been sought to elucidate the nature of the petals—whether they are akin to sepals or stamens. Thus Goebel (1933) correlates the belated appearance of petals during the ontogeny of the flower with their nearness to stamens. In the orchids the ontogenetic order of appearance of floral whorls is centripetal (Swamy, 1946; also unpublished data). And even when Goebel's correlation is applied to the condition in orchids, it is seen that the petals are not allied to stamens but to sepals.

LABELLUM. This structure of the orchid flower has been the target for much dispute. Brown (1831) put forward the doctrine that the labellum is a compound structure resulting from the fusion of some of the staminal members with the lip. However, he did not offer sufficient evidence for his opinion and also was not certain as to which of the stamens enter into fusion. He further suggested that such a fusion was especially responsible for the extra-conspicuousness of the labellum with ridges and crests in some orchids. Lindley (1840) followed this view. Darwin (1899), after studying the course of vascular traces in some orchids, came to the same conclusion: "The Orchid flower consists of five simple parts, namely, three sepals and two petals; and of two compound parts, namely, the column and labellum. The column is formed of three pistils and generally of four stamens, all confluent. The labellum is formed of one petal with two petaloid stamens of the outer whorl, likewise completely confluent." As Darwin thus elaborated and confirmed Brown's ideas, the authorship of the compound theory

of the labellum is attributed both to Brown and Darwin (see Fig. 11, which gives a diagrammatized interpretation of a monandrous orchid flower according to Darwin's conception).

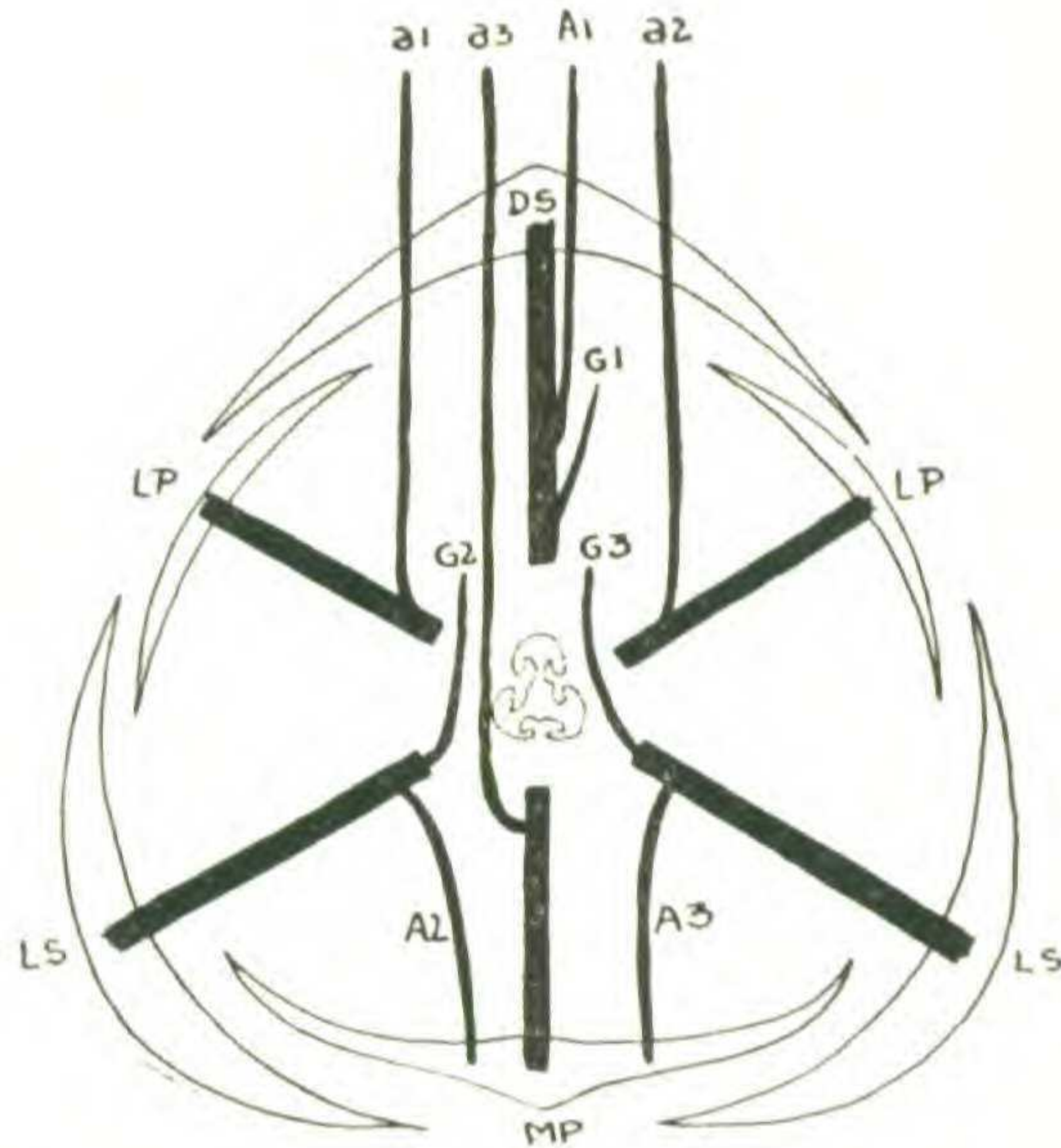


Fig. 11. Vascular diagram of a monandrous orchid flower reconstructed according to the description of Darwin.

The Brownian and Darwinian conception of the orchid labellum held sway for a long time, influencing subsequent studies to a great extent. Many reports on teratological orchid flowers were interpreted in the light of this hypothesis and were brought forward as evidences in favor of it. Even as recently as 1937, Saunders, while attempting to advocate her theory of "carpel polymorphism," fully accepted the old hypothesis, ignoring the opposition brought forward in refutation of the Brownian and Darwinian views of the orchid labellum.

Crüger's views (1865) which are contrary to the compound concept of the labellum seem to have been ignored until 1916, when Worsdell brought out his two volumes of "Principles of Plant Teratology." In this publication, Worsdell has accumulated all of the points adduced in favor of the compound nature of the labellum and has

given his own alternative interpretations of the very examples which were previously interpreted as evidencing the old hypothesis. He also summarizes other instances "which decidedly seem to tend towards disapproving the accepted theory and to support that advanced by Crüger." In addition to these, he presents some of his own original observations on some abnormal flowers of *Cypripedium*. All of these combine to support the opinion that there is not even a single instance to support the view of the compound nature of the labellum.

As can be seen, until now the Brownian and Darwinian concept of the orchid labellum has largely been checked only with teratological flowers. Excepting the study of Masters (1887), which deals in part with the vascular anatomy of normal flowers, I am not aware of other subsequent contributions dealing with the anatomical studies of normal orchid flowers.

The present anatomical study of 40 species of orchid flowers belonging to 24 genera also does not show any evidence in support of the compound theory of the labellum. The traces representing the lateral stamens of the outer whorl, whenever present, are distinctly identifiable in the gynostemium. Their independent origin and course is especially clear in forms like *Eulophia*, where no kind of secondary fusion nor complication accompanies their expression. Even in those instances where adnation results in a compound staminal supply as $a_1 + A_2$ and $a_2 + A_3$, the traces without an exception pass into the gynostemium but not into the labellum. Furthermore, the labellum is almost always provided with separate marginal traces, given out by the veins belonging to the adjacent perianth members. As has already been stated in an earlier part of this text, the labellum receives typically a median and two marginal traces and hence is in no way different anatomically from other perianth members.

From a consideration of these facts, the only reasonable conclusion that can be arrived at is that the labellum is not a compound structure as was supposed by Brown and Darwin. It may also be noted here that those instances in which the marginal traces of the labellum were not in evidence or exhibited abnormal behavior when present offered difficulties of interpretation to Darwin himself. For he writes: "This anomaly is so far of importance, as it throws some doubt on the view that the labellum is always an organ compounded of one petal and two petaloid stamens."

SPUR. This structure, as has been explained already, is a basal outgrowth from the labellum in the form of a pouch, sac or narrow tube. Where the spur is single, the median trace of the labellum continues into it and then recurves upwards in conformity with the curvature of the spur to constitute the median trace of the same petal. When the spur is double, the median trace of the labellum does not enter the spur but each marginal trace enters into the spur of the corresponding side. In passing, it may be mentioned that Darwin thought the traces that traverse the double spurs were staminal (A2 and A3). That Darwin's views are untenable has already been made clear.

GYNOSTEMIUM. This is a structure peculiar to the orchid flower. Its exact nature has, until now, been little understood. Chiefly the works of Oliver (1895), Rendle (1930) and Willis (1936) have propagated the idea that this structure is an extension of the floral axis and that on this account it is to be looked upon as being axial. It may be recalled that such a distinct structure is not clearly evidenced in *Cypripedium*, *Habenaria*, etc. In the former, it is incipient if it is present at all; serial

microtome sections alone can reveal its incipient condition anatomically. In all of the other orchid flowers studied at this time the structure is well-developed; and in all such species, it is an appendicular structure containing the vascular traces supplying the staminal and stigmatic whorls. The morphological apex of the flower, therefore, does not extend to the apex of the gynostemium but ceases at the point of the insertion level of the perianth. Thus, in one and the same "floral tube" (as designated by Wilson and Just, 1939) of orchids, different degrees of adnation are seen, the ovary proper containing the fused vascular traces of all of the floral whorls and the gynostemium proper in which the individual traces of the stamens and stigmas are embedded.

STAMENS. Robert Brown (1831) was the first to state in clear terms that the stamens in the orchid flowers are arranged in two alternating whorls, each whorl containing three stamens. Since then Darwin's investigations (1899) on several other orchids have brought to light a certain amount of evidence to support Brown's views. But as Darwin also believed that the lateral stamens of the outer whorl were fused with the labellum, he contemplated that only the lateral stamens belonging to the inner whorl were always present in the gynostemium.

It is not so easy to determine which particular trace represents which particular stamen just by observing a section of the gynostemium. "Compound" staminal traces have been demonstrated in the present study as a very common condition in orchid flowers. Some other salient points concerning the vascular supply to the stamens may now be recalled:

(1) In the *Cypripedilinae*, a1 and a2 are normally present and are functional. A1 is transformed into a staminode. In teratological flowers (see Worsdell, 1916)

sometimes A2 or A3 or even a3 may be represented by the corresponding staminodal outgrowths externally or by vascular traces internally.

(2) In the Ophrydinae it has been shown here that A1 alone manifests itself as the functional stamen and that no other stamens are represented even by vascular traces.

(3) In the remainder of the members of the Monandreae, as a rule, A1 is the functional stamen, a1 and a2 or sometimes A2 and A3, being present as traces. The origin and course of the various staminal traces (excepting the one pertaining to A1) may be somewhat irregular in some advanced genera. They may be quite clear in the juvenile condition of the flower but later become obliterated, or they may be "compound" from the very beginning. In the majority of the genera, however, all of the four lateral stamens are represented by the "compound" traces, a1+A2 and a2+A3.

(4) The expression of a3, though rare, can still be seen in some instances.

The above facts, when considered from an "over-all" point of view, account for the presence of all of the six stamens belonging to the two whorls. At one time, perhaps, all of the six stamens were functional. During phylogenetic specialization, the median one of the inner whorl (a3) disappeared early, probably in correlation with the differentiation of the labellum. Subsequently, the elimination of the lateral stamens of the outer whorl was effected first and of the inner whorl later; this is suggested by the more frequent predominance of the latter and the less frequent expression of the former among the orchids here studied. However, when the vascular traces of the lateral stamens of both the whorls are present, they form "compound" traces as a1+A2 and a2+A3.

A study of the published floral diagrams of *Neuwiedia* (Pfitzer, 1889) reveals that an early step in the suppression of the three stamens of the posterior half of the flower (A 2, a3 and A 3) had already started here; hence the functional stamens were the median one of the outer whorl (A 1) and the lateral stamens of the inner whorl (a1 and a2). Such flowers specialized further along two distinct lines: (1) suppression of the median stamen of the outer whorl (A 1), which tendency gave rise to forms like the diandrous orchids, and (2) suppression of the lateral stamens of the inner whorl (a1 and a2) which tendency resulted in monandrous orchids. Such an interpretation is in conformity with the stand taken by Rolfe (1909-12). (These aspects are fully discussed in my paper, "Embryological studies in the Orchidaceae, Part II," which is under publication).

CARPEL. According to the classical view, the orchid ovary is unilocular and tricarpellary; the ovules are marginal, the margins of the adjacent carpels having fused to such an extent as to obliterate the double nature of the ovule-bearing vascular traces. The median trace of each carpel supplies the respective stigma.

The only opposition to the above-mentioned view is that advanced by Saunders (1923, 1937). She contends that each of the main vascular traces of the ovary represents a carpel; that the main traces underlying the outer whorl of perianth are to be considered as solid sterile carpels bearing stigmas and that the main traces underlying the inner whorl of perianth members are to be considered as representing semi-solid carpels where placentae have approached the median trace of the carpel.

There is absolutely no anatomical evidence to favor Saunders' views. The inconsistencies and irrelevancies of the theory of "Carpel Polymorphism" have been

brought to light repeatedly by several workers in several plant families. So it becomes unnecessary to consider Saunders' attack with any seriousness.

However, one difficulty that may be postulated against favoring the classical view of the orchid carpel is that of the irregularity of the origin and differentiation of the median and marginal traces of each carpel. But this objection, if it can really be called an objection, will be nullified when we take into consideration the high degree of anastomoses, cohesion, adnation and other allied phenomena accompanying the structural evolution of the flower.

SUMMARY

The orchid ovary is traversed by six main vascular traces. In the *Cypripedilinae*, the origin and subsequent development of these six traces are not attended by any secondary modifications. But among the monandrous genera, a series of increasingly complex and diverse patterns is witnessed; thus the number of vascular bundles that enter into the construction of the flower from the inflorescence axis is usually three, but this may be reduced to two; their method of breaking up into the six main traces of the ovary also is highly diverse in different genera. None of the main traces of the ovary show any signs of supply either to the placentae or to the ovules. The main traces begin to break up and supply the other floral members only at the upper extremity of the ovary.

Depending largely upon the presence or absence, number and nature of the vascular traces supplying the stamens, three types of vasculature of orchid flowers are recognized: Type I, characterizing the *Cypripedilinae*, Type II, characterizing the *Ophrydinae* and Type III, characterizing the rest of the *Monandrae*.

It is Type III that presents an interesting series of increasing complexity. The latter is intimately associated with anastomoses, cohesion and adnation of the individual vascular traces of the flower. The increasing trend of complexity of perianth members is seen in the derivation of marginal traces of the perianth members of one whorl from those of the other and their anastomoses. As a result of this, the places of origin of the staminal traces become highly displaced and carried to higher levels, until the adjacently placed lateral staminal traces form "compound" traces, here designated as $a_1 + A_2$ and $a_2 + A_3$. The effect of adnation on the different whorls of the flower has been described in detail.

The inferior ovary is looked upon as due to an extreme adnation of the different floral whorls. The outer and inner whorls of the perianth, though externally distinct from one another, present the same anatomical features and on this account the inner whorl is considered to be more sepaline than otherwise. The labellum is also shown to receive the same vascular supply as the rest of the perianth members; it is stressed that there is no evidence to consider it to be a compound structure, as was thought by Brown and Darwin.

The two lateral stamens of the outer whorl which were thought by Darwin to have fused with the labellum, are here shown to be represented in the gynostemium, either as individual traces (A_2 and A_3) or in their "compound" manifestations ($a_1 + A_2$ and $a_2 + A_3$), whenever they are present. It has also been shown that the median stamen of the inner whorl is capable of expressing itself occasionally.

It is suggested that in the ancestral orchid flower all of the six stamens were functional; that in course of time the posterior three ceased to be functional and that it seems as if such a progenitor may have given rise to the

Diandrae on the one hand and the Monandrae on the other.

Evidence is presented in favor of the appendicular theory of the gynostemium, in opposition to the views of those who consider it to be a prolongation of the floral axis.

I am very thankful to Professor R. H. Wetmore for kindly reading the manuscript and offering valuable suggestions for improvement in presentation.

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